

# A model for predation pressure in colonial birds

J. L. Tella\*, M. A. R. de Cara\*,<sup>†</sup>, O. Pla<sup>†</sup> and F. Guinea<sup>†</sup>

\* *Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Avda. M<sup>la</sup> Luisa s/n, E-41013 Sevilla, Spain*

<sup>†</sup> *Instituto de Ciencia de Materiales de Madrid, Consejo Superior de Investigaciones Científicas, Cantoblanco, E-28049 Madrid, Spain*

**Abstract.** Different explanations have been proposed for the existence of colonial breeding behavior in birds, but field studies offer no conclusive results. We analyze the interplay between learning habits and predation pressure by means of numerical simulations. Our analysis suggests that extremely simple learning processes and equally simplistic models of predation pressure lead to the formation of stable colonies.

## INTRODUCTION

Colonial breeding behavior in birds has been extensively studied [1–3]. Different hypotheses have been put forward in order to explain this behavior, like minimizing the distance required for foraging [4], observation of conspecific foraging groups [5], information transfer at the colony [6], shortage of nests [7,8], or predation pressure [1].

One of the difficulties in verifying the previous hypotheses is that present day conditions need not coincide with those which lead to colonial behavior in the first place. Thus, modelling of bird populations using reasonable assumptions for bird behavior can be useful in the elucidation of possible scenarios favorable towards the evolution of coloniality.

Some theoretical studies give support to the hypothesis that information transfer at the colony increases the tendency towards colony formation [9–11].

Predation can induce colonial habits in many ways. The simplest passive mechanism is the dilution effect provided by a colony of sufficiently large size [12–14]. In addition, the detection and defense capabilities are enhanced in colonies [12,14–17]. On the other hand, the lack of significant predation pressure on some colonial species has been used as evidence against the predation hypothesis [13,18], although a phylogenetic analysis of coloniality across bird species shows a strong correlation with exposure to predation [3].

The present work analyzes the role of predation on the formation of colonial habits by means of a mathematical model which incorporates some of the known facts about the response of birds to attacks by predators, and makes simple assumptions about the memory and learning processes at play.

## THE MODEL.

We assume that the available choices to birds is limited to two possibilities each breeding season: they can either form an individual nest, or join an existing colony. This binary restriction allows us to make use of the extensive literature on competition and collective behavior of agents with bounded rationality [19, 20].

Successful breeding individualstend to be faithful to their previous nesting site. Birds choose a colony or an isolated nest depending on their previous experience. This experience is modelled in a similar way to that used in the so called “minority game” [20, 21]. Each bird has, as already mentioned, two strategies. Each of these strategies has a score, which reflects the degree of reproductive success that the bird would have had if it had followed it. In this sense, the model departs from the minority game usually analyzed in the literature, where the score of strategies is the same for all agents. The present version reflects the diversity of birds, due to genetic differences and other sources, and resembles the “individual” version of the minority game [22].

A bird who made a succesful choice assigns the achieved score to its available strategies whose outcome is the same choice that it has taken. On the other hand, a bird whose nest is predated increases the score of those strategies whose outcome is the opposite.

Individual strategies, when succesful, obtain a larger score than colonial strategies (2 vs. 1), reflecting the ancestral tendency of birds to solitary breedingin the absence of predation. The number of sites is much larger than the number of birds. Unless otherwise stated, the predation probability,  $p_{pr}$  fluctuates between 0 and a given value,  $p_{max}$ . In this way, we model the natural variability of the abundance of predators.

At each time step, which corresponds to one breeding season, there is a finite probability that a nest will be predated. Predation of nests in a colony of size  $N$  is reduced by a factor proportional to  $N$ . We do not follow the detailed evolution of individual colonies in the habitat. Instead, we assume that there is a fixed distribution of colony sizes, such that the probability of finding a colony of a given size is inversely proportional to its size. This is the expected behavior if the relative fluctuation of colony sizes is random. The distribution is normalized to the total number of birds that have colonial behavior.

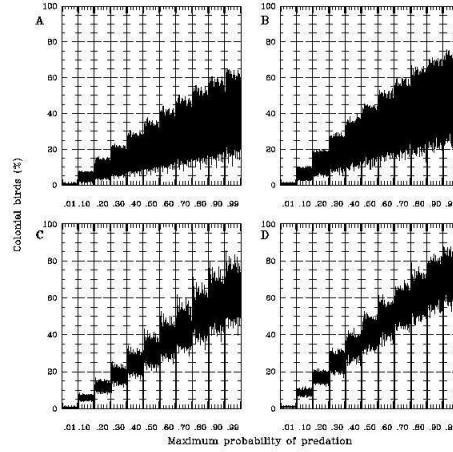
We model the birds’ finite lifespan by setting the score of the strategies of a given bird to zero with some finite probability,  $p = \frac{1}{v}$ , at each time step. This implies that a bird has been replaced by a new one with no previous experience. The total population is kept constant.

## RESULTS.

We show, in fig. (1), the number of colonial birds, as function of time, for different values of  $p_{max}$ , and two lifespans (3 and 10 years). The number of birds is 10000. In the absence of predation, individual strategies acquired two points per season, while colonial behavior was awarded one point, reflecting the genetic tendency towards individual nests.

Finally, we have considered two possible behaviors: a) each individual may check the scores of all its strategies, and uses the one with the highest score every breeding season. Thus, birds would rely its decisions on their long-term previous experience (*long-term experience*). b) If the nest of a given individual was not predated during the previous season, it repeats the last choice. If the nest was predated, the individual acts as in behavior (a).

All birds were located in individual nests at  $t = 0$ , and we have followed the evolution of the population during  $10^4$  time steps.



**FIGURE 1.** Evolution of the number of colonial birds, as function of time, for different maximum predation pressure. Top graphs: Short-lived species relying on (A) their long-term previous breeding experience, and on (B) their immediate previous breeding experience. Bottom graphs: Long-lived species relying on (c) their long-term previous breeding experience, and on (D) their immediate previous breeding experience.

## CONCLUSIONS.

Our results suggest that colonial behavior can arise as a natural response to predation pressure. Note that we made a number of conservative assumptions, in order to avoid any bias towards colonial behavior: i) The birds have an innate tendency towards preferring individual nests, ii) The only protection provided by the colony is the dilution effect, iii) The distribution of colonies is such that small colonies are more abundant, and iv) predation pressure fluctuates strongly from year to year, allowing for the existence of periods of low predation.

The number of colonial birds increases with increasing lifespan, as birds accumulate experience for a longer period. This evidence is in agreement with the observation that birds make use of their long term breeding experiences [23–26].

## REFERENCES

1. Lack D., *Ecological adaptations for breeding of birds*, London: Chapman and Hall, 1968.
2. Siegel-Causey, D., and Kharitonov, S. P., *Current Ornithology* **7**, 285 (1990).
3. Rolland, C., Danchin, E., and de Fraipont, M., *American Naturalist* **151**, 514 (1998).
4. Horn, H. S., *Ecology* **49**, 682 (1968).
5. Thorpe, W. H., *Learning and instinct in animals*, London: Methuen, 1956.
6. Ward, P. and Zahavi, A., *Ibis* **128**, 195 (1973).
7. Snapp, B. D., *Condor* **78**, 471 (1976).
8. Shields, W. M., and Crook, J. R., *Ecology* **68**, 1373 (1987).
9. Bouchamp, G., and Lefebvre, L., *Journal of Theoretical Biology* **132**, 357 (1988).
10. Barta, Z., and Szép, T., *Behavioral Ecology* **6**, 308 (1995).
11. Buckley, N. J., *American Naturalist* **149**, 109 (1997).
12. Veen, J., *Behaviour Supplements* **20**, 1 (1977).
13. Burger, J., *Quarterly Review of Biology* **56**, 143 (1981).
14. Tella, J. L., Ph. D. dissertation, Barcelona (1996).
15. Kruuk, H., *Behaviour Supplements* **11**, 1 (1964).
16. Hoogland, J. L., and Sherman, P. W., *Ecological Monographs* **46**, 33 (1976).
17. Arroyo, B., Ph. D. Dissertation, Oxford (1995).
18. Forbes, L. S., *Colonial Waterbirds* **12**, 24 (1989).
19. Arthur, W. B., **Amer. Economists Assoc. Papers and Proceedings** **84**, 406 (1994).
20. Zhang, Y.-C., *Europhysics News* **28**, 51 (1998).
21. de Cara, A. R., Pla, O., and Guinea. F., *Eur. Phys. Journal B* **10**, 187 (1999).
22. de Cara, A. R., Pla, O., and Guinea. F., *Eur. Phys. Journal B* **13**, 413 (2000).
23. Southern, W. E., Patton, S. R., Southern, L. K., and Hanners, L. A. *Auk* **102**, 827 (1985).
24. Bollinger, E. K., and Gavin, T. A., *Auk* **106**, 584 (1989).
25. Thompson, P. S., and Hale, W. G., *Ibis* **131**, 214 (1988).
26. Oro, D., Pradel, R. and Lebreton, J.-L., *Oecologia* **118**, 438 (1999).